A REVIEW OF THE GENUS ECCREMOCARPUS (BIGNONIACEAE)1,2

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GENTRY INVITATION SERIES

This is the first of a series of publications paying tribute to or using data left by the late Alwyn H. Gentry, who died in an airplane crash in Ecuador on August 3, 1993. The Bignoniaceae had been his primary monographic theme. From a base at the Missouri Botanical Garden, Gentry traveled to many parts of the world conducting field and herbarium studies of this family. Some of his best known taxonomic work appeared in the Flora Neotropica series and in the floras of Panama, Veracruz, Ecuador, and Venezuela. A summary of his life and scientific contributions, with a complete list of his publications, was provided by James S. Miller and collaborators in the Annals of the Missouri Botanical Garden volume 83, number 4.

Among materials left by Gentry is a computer database with information from some 55,000 collections he had examined from more than 122 herbaria around the world. He also left a series of unpublished manuscripts, including

a treatment of the Bignoniaceae of Colombia, which is to be published in the Flora de Colombia series.

Others are encouraged to explore and utilize the rich legacy left by Al Gentry. This Invitation Series is being established for taxonomic publications by people who are relying on material left by Gentry, or who wish to pay tribute to other contributions he made to their work. Those interested should contact William G. D'Arcy at the Missouri Botanical Garden for details.—WGD

ABSTRACT

Eccremocarpus is a genus of three species that grow in the uplands of Andean South America. The plants are vines with showy flowers. Morphology divides the genus into two groups that are also geographically separated: section Eccremocarpus and section Calampelis. This paper reviews the work left by the late Alwyn H. Gentry and that of others and reduces the number of species from former concepts to three. A key to the species and a map of their distribution are provided.

The genus Eccremocarpus is distinct from other Bignoniaceae in its dissected leaves, parietal placentation, and aseptate, dehiscent capsules, and it forms its own tribe, the Eccremocarpeae. It is also distinct in its elevational range, which is well above that of the rest of the family. Eccremocarpus includes three species forming two distinctive species groups. One of these, section Eccremocarpus, occurs in Colombia, Ecuador, and Peru. It includes plants of variable appearance but only two clearly distinguishable species, Eccremocarpus huainaccapac and E. viridis. The other, section Calampelis, with one species, E. scaber, occurs in Chile and Argentina and its plants show less variability.

HISTORY

Eccremocarpus was first described in 1794 by Ruiz and Pavón, who soon after (1798) described

two species, Eccremocarpus viridis from Peru, and E. scaber from Chile. Eccremocarpus scaber was recognized in 1819 by D. Don as a separate genus, Calampelis, which effectively lectotypified Eccremocarpus with E. viridis. The first description and figure of Eccremocarpus by Ruiz and Pavón is of E. viridis and not of E. scaber. Other species described by subsequent botanists, some in other genera, are dealt with below.

Macbride (1961) treated the genus in the Flora of Peru, recognizing three species.

Eccremocarpus was revised by Sandwith (1965), who hesitantly recognized six species and placed them into two sections, sect. Eccremocarpus with five species, and sect. Calampelis with only E. scaber. Sandwith provided a description only for his new E. vargasianus.

¹ This paper is number 1 of the GENTRY INVITATION SERIES, in acknowledgment of contributions to the study of the Bignoniaceae made by Alwyn H. Gentry.

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Muñoz (1966) provided a description and illustration of the Chilean *Eccremocarpus scaber*, reducing the variety *sepium* to synonymy.

The late Alwyn H. Gentry, whose aborted monographic studies of the Bignoniaceae this paper commemorates, followed the taxonomy of Sandwith. In publication, Gentry treated one species, Eccremocarpus longiflorus, in his floras of Ecuador (1977) and Colombia (in press), and he listed E. huainaccapac, E. longiflorus, E. scaber, E. vargasianus, and E. viridis for Peru (Brako & Zarucchi, 1993). These species also appear as determinations in his computerized database. However, Gentry made no reference to one species recognized by Sandwith, E. lobbianus Zahlbr. This element is known by scant material in Europe, and it may not have been studied by Gentry. Gentry provided a description only for E. viridis (as E. longiflorus, see Gentry 1977).

Careful review of most of the material seen by Sandwith and Gentry, and some additional collections not seen by them, has led me to the hesitant conclusion that Eccremocarpus lobbianus, E. longiflorus, E. vargasianus, and E. viridis are variants within a single species that should be known as E. viridis. It cannot be known whether Gentry might have continued to follow Sandwith's concepts had he lived to revise the genus as a whole, but in other treatments, he did tend to have a narrower species concept than the present author. Unfortunately, none of the students of the genus as a whole, Sandwith, Gentry, and the present writer, collected or is known to have seen wild populations of Eccremocarpus, although Sandwith may well have seen cultivated plants at Kew. This treatment departs from the Sandwith/Gentry concept in recognizing only three species, but in deference to the previous tradition, indication is made of how taxa and collections were viewed by these earlier workers. In citations that follow, reviewers of specimens are indicated by superscripts as: S N. Y. Sandwith, G A. H. Gentry, 'present author. No symbol means not seen by any of these.

SYSTEMATICS

The tribe Eccremocarpeae was established by A. De Candolle (1845) to embrace the single genus *Eccremocarpus*. This concept has been followed by later workers (Sandwith, 1965; Gentry & Tomb, 1979 [1980]).

Tribe Eccremocarpeae is characterized as having a 1-locular ovary with two bifid, parietal placentas (Gandhi & Thomas, 1983), a loculicidal capsule that remains fused apically, and winged seeds. The plants are vines with opposite, dissected leaves and tendrils (Melchior, 1964: 456). Gentry and Tomb (1979 [1980]) reported similarities in the pollen of *Eccremocarpus* to that of *Jacaranda* of tribe Tecomeae and to that of *Tourettia* of tribe Tourrettieae. The fruit in tribe Tecomeae also is loculicidal.

Two groups are clearly identifiable in the genus. Section Calampelis comprises the small-flowered, relatively uniform Eccremocarpus scaber, which is represented by abundant collections mainly from Chile. Section Eccremocarpus comprises plants similar to the type species, displaying larger flowers and fruits than in section Calampelis. These plants are found to the north of Chile in Peru, Ecuador, and Colombia, and they are known by fewer, more variable collections. Main differences between the two groups are given in the key to species.

The reduction of section *Eccremocarpus* into two species is done with some hesitation, especially as it breaks with the Sandwith/Gentry tradition of recognizing four or five species. Judging from the few color photographs seen, different morphs of *E. viridis* look very different, an impression stemming mainly from striking color differences in the calyces and differences in flower dimensions. Corolla length appears to differ considerably within the same inflorescence. The varying flower colors reported in cultivated plants of *E. scaber* invite suspicion that colors are variable in the northern species, too. Separating characters noted in Sandwith's key, such as pubescence and flower length, display continuous or overlapping patterns.

Eccremocarpus huainaccapac is closely related to E. viridis and shares many characters with it, but it is distinguished by its dense, glaucous-drying overall pubescence and its slightly larger leaflets. A much weaker case might also be made for recognizing Eccremocarpus vargasianus, but the evidence seen does not commend this view.

GEOGRAPHY

Eccremocarpus is found in the Andes of South America. Northern collections from Colombia, Ecuador, and Peru (E. viridis, E. huainaccapac) occur mainly between elevations of 3200 and 3700 m, and southern collections from Chile and southern Argentina (E. scaber) occur mainly from 1000 to 1800 m. This distribution is shown in the map of Figure 1. To judge by collections seen, populations are widely scattered and morphologically variable. Similar patterns occur in many other wind-dispersed groups in Andean uplands, for example, Mnioides (Asteraceae), Niphogeton (Apiaceae), Puya (Bromeliaceae), and Polylepis (Rosaceae).

SOUTH AMERICA

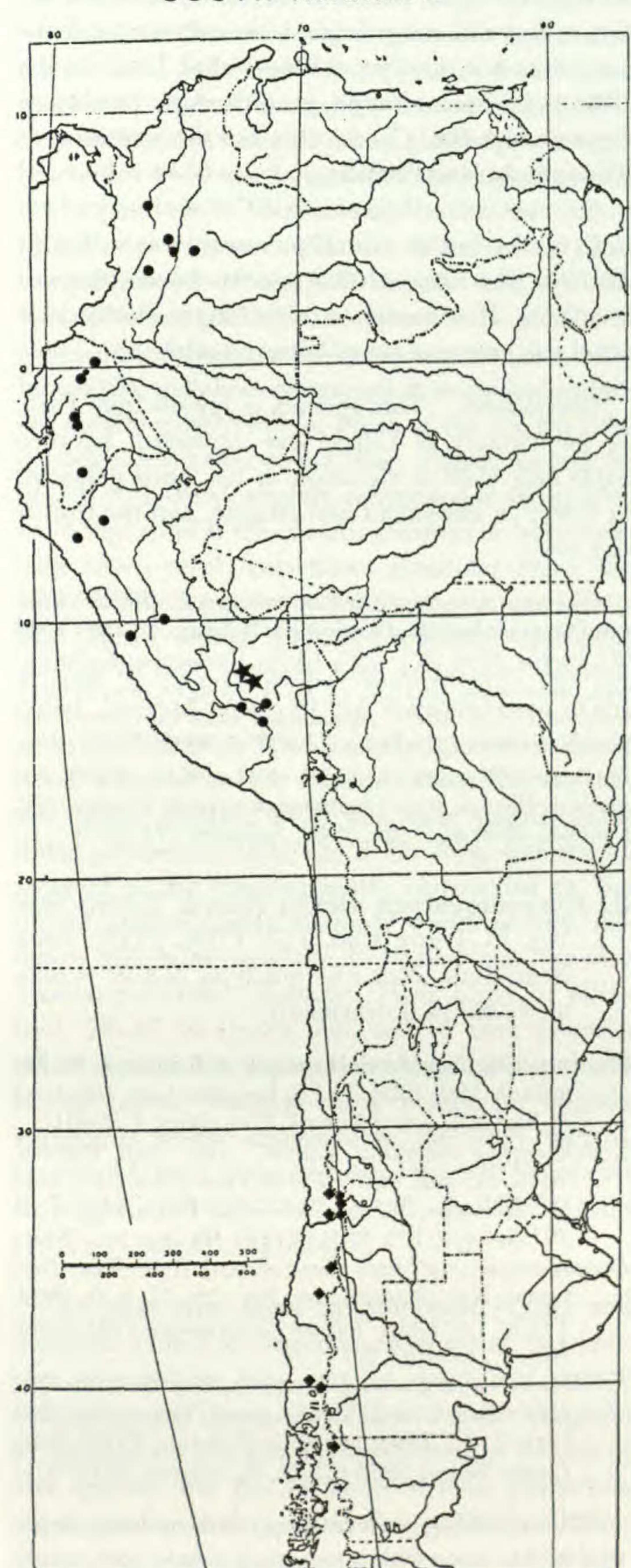


Figure 1. Map of western South America showing distribution of Eccremocarpus species. Diamonds = Eccremocarpus scaber. Stars = Eccremocarpus huainaccapac. Circles = Eccremocarpus viridis. The collection of E. scaber indicated in Peru is dubiously from a wild plant.

"We may generalize that wide-ranging species are the rule rather than the exception for much of the neotropical flora, especially in wind-dispersed groups" (Gentry, 1979: 342).

TAXONOMIC TREATMENT

Eccremocarpus Ruiz & Pavón, Prodr. Fl. Peruv. Chil. 90. 1794. TYPE: Eccremocarpus viridis Ruiz & Pavón.

Calampelis D. Don, Edinb. Phil. Jour. 7: 89. 1829. TYPE:

Calampelis scaber (Ruiz & Pavón) Sweet = Eccremocarpus scaber Ruiz & Pavón.

Vines, subfrutescent, stems without anomalous vasculature, ridged and sulcate on drying, without pseudostipules or interpetiolar glands. Leaves opposite, bipinnatisect or tripinnatisect, a much branched tendril terminal on the leaf. Inflorescences racemose, generally reduced to a few flowers. Flowers with the calyx showy, often red or pink, campanulate with 5 sutures reaching near the middle, glabrous or puberulent; corolla showy, tubular, slightly curved or ventricose, sometimes contracted apically and almost urceolate, the lobes small, glabrous to pilose outside; anthers slightly exserted or situated just below the mouth of the tube, the anther medifixed and the thecae parallel or fixed near the apex and divergent; ovary ovoid or conical, unilocular, the ovules multiseriate on two parietal placentas; disc annular-pulvinate. Fruit an ovoid to ovoid-ellipsoidal capsule, the calyx persistent, unilocular, with two narrow valves that remain connected; seeds plane, suborbicular, the narrow membranous wings circling the body of the seed.

Etymology. Greek ekkremes = pendulous, and karpos = fruit.

KEY TO SPECIES

- 1'. Flowers mostly more than 3 cm long; calyx more than 15 mm long; fruit base hidden in the calyx; leafy part of stems pilose; pubescence mostly eglandular, hairs to 4 mm long; leaves opposite; leaflets mostly sessile or held close to the rachis, entire or grossly lobed with one principal nerve from the base and 2–3 strong lateral nerves; plants from Peru, Ecuador, or Colombia. Section Eccremocarpus.

- Plants tomentose; stamens five 1. E. huainaccapac Plants glabrate; stamens four 2. E. viridis (includes E. lobbianus,
 - E. longiflorus, E. vargasianus)

Eccremocarpus sect. Eccremocarpus

1. Eccremocarpus huainaccapac Vargas, Bol. Soc. Peru. Bot. 1: 15. 1948. TYPE: Peru. Cuzco: Quesser-huailla, 3900-4000 m, Vargas 3034 (holotype, CUZ; isotypes, Ks, USsc).

Vine, the stem with alternating ridges and canals, pilose with copious erect weak, mostly eglandular hairs of varying length to 2.5 mm. Leaves opposite, generally 3-6 cm long, bipinnate with opposite pinnae, each with a terminal, ternately branched tendril and usually three primary alternate pinnae, leaflets subentire or lobed to pinnatisect and appearing 3-foliolate, mostly oblique and appearing rhombic, the terminal leaflet largest, 8-12 × 3-5 mm wide, proximal leaflets often ovate or elliptical, pilose with weak simple, light colored multicellular hairs to 1 mm long, more so beneath, discolorous, dark above; petiolules 1-2 mm long, pilose; petiole 2-6 cm long, glabrate or granular-pubescent. Inflorescences leaf-opposed, racemose, several to many flowered, to 14 cm long, pubescent with simple gland-tipped hairs; bracteoles ca. 10 mm long, ovoid, apically obtuse; pedicels 5-15 mm long, pilose. Flower buds narrowly ovoid; calyx campanulate, 8-10 × 13-15 mm, 5-dentate, split 1/3-1/2 way down, pilose with gland-tipped hairs; corolla basally campanulate, 40-45 mm long and 2-3 mm wide within the calyx, above cylindrical, pilose overall outside, minutely pilose basally within, 7-8 mm wide at the mouth, the lobes green, obtuse, ca. 4 mm long, glabrate; stamens 5, unequal, the filaments inserted ca. 7 mm from the base, free, sparingly pubescent at point of insertion, the anthers unequal, 5-10 mm long (in the same flower), dorsifixed near or above the middle, thecae separate but parallel below the insertion point; style exserted ca. 4 mm, the lower stigma lobe reflexed, ovary sessile, ovoid, with two pronounced longitudinal ridges, 4 mm long, the surface granular; disc annular-pulvinate with a few minute distal trichomes, ca 1.5 mm tall, ca. 6 mm wide. Fruit not known. Figure: Vargas (1948: 15, 16).

In the one flower examined (Nuñez & Galiano 13414), the shorter stamens may lack pollen. The stamens were unequal in size, and the corolla was exserted from the calyx by only 1.5 cm, suggesting that the flower was not yet fully expanded into anthesis.

Vargas (1946: 47) listed the species in Diez Años

al Servicio de la Botánica en la Universidad del Cuzco, but did not provide a description, and the name was not validly published until 1948. In the 1946 publication, Vargas gave the type locality as Qquesser-huailla, Ckoricocha, but the specimen at US reads Igneser-Huailla.

Eccremocarpus huainaccapac is similar in form to E. viridis, but its overall pubescence is strikingly distinct. The name of this species honors the last Inca king, Huainacapacc (sic). Vargas (1948) supplied the common name "Chucchucha."

Distribution. This species is known from Peru, in the vicinity of Cuzco and Apurimac between 3100 and 4100 m elevation. It has been collected in flower in December and August, and the fruit is unknown.

All known specimens (E. huainaccapac). PERU. Cuzco: Qquesser-huailla, Ckoricocha, N Cuzco, 24 Dec. 1942 (fl), Vargas 3034 (Ks!, USGs, CUZ); Urubamba, Kello Cocha, Yanacocha, 13°15'S, 72°16'W, 4150 m, (fl), Nuñez & Galiano 13414 (MOG!). Apurimac: Grau Province, Interandean valley of Coyllurqui, 13°50'S, 72°25'W, 3165 m, 26 Aug. 1991 (sterile), Nuñez et al. 14135 (MOG!); Aymaraes, 160 km from Challhuanca towards Puquio, dist. Cotarosi, 4050 m, 7 Jan. 1962, Saunders 776 (KGS!).

2. Eccremocarpus viridis Ruiz & Pavón, Syst. Veg. Fl. Peruv. Chil. 157. 1798. TYPE: Peru. Near Muña, Ruiz s.n. (holotype, MA- 2^s = photo, F-29234, F-fragment).

Eccremocarpus longiflorus Humboldt & Bonpland, Pl. Aequin. 1: 229. 1808. TYPE: Ecuador. Loja: Humboldt & Bonpland s.n. (holotype, P = photo, F-39401).

Eccremocarpus lobbianus Zahlbr., Ann. Nat. Hofmus. Wien, 12: 103. 1897. TYPE: Peru ("Bolivia"), Lobb s.n. (holotype, Ws fide Sandwith, 1965: 148), Lobb 391 (isotype, Ks!). PARATYPE: Maclean s.n. (Ks!).

Eccremocarpus mutisiana Cuatrecasas, Trab. Mus. Nac. Cienc. Nat. (Madrid), ser. Bot. 26: 15, f. 9. 1933. TYPE: Colombia. Tolima: Cuatrecasas 2743 (holotype, F!, isotypes, K!).

Eccremocarpus vargasianus Sandwith, Kew Bull. 19: 406. 1965. Based on E. viridis sensu Vargas, Bol. Soc. Peru. 1: 15. 1948, non Ruiz & Pavón. TYPE: Peru. Cuzco: Vargas 5956 (CUZ?, K, isotypes MO-2^{G!}).

Vine climbing and twining, 2-4 m long, semiwoody, the stem with alternating ridges and canals, glabrate with sparse inconspicuous ascending eglandular hairs, erect gland-tipped hairs and reduced hairs present on emerging growth, sometimes persistent at the nodes. Leaves opposite (sometimes one reduced or suppressed), generally 3-6 cm long, bipinnate with opposite pinnae, each with a terminal, mostly 3 times branched, wiry tendril, usually with four primary alternate pinnae, leaflets ovate or elliptical to cordate or rhomboid, 3-7(-9) mm long, 1.5-25 mm wide, glabrate to short-glan-

dular-pilose; petiolules 2-5 mm long, often pubescent; petiole 2-6 cm long, or glabrate or granularpubescent. Inflorescences opposite the leaves, racemose, several flowered, to 16 cm long, pubescent with short, simple, erect, gland-tipped hairs; bracteoles 4-10 mm long, deltoid to linear, apically acute; pedicels 5-15 mm long, the flowers twisting to one side. Flowers with the calyx red or pink, campanulate, 8-10 × 13-30 mm, 5-lobed, split 1/3-1/2 way down, glabrous to pilose with simple or gland-tipped hairs, sometimes nervate, the lobes lanceolate and short-acuminate to ovate and rounded; corolla mostly yellow, green at the tip, the tube cylindrical, broader at the base, slightly curved, 3- $8(-12) \times 1-3$ cm, slightly contracted at the mouth, ca. 4 mm wide at the mouth, glabrous or pubescent with short, erect, sometimes glandular hairs, the lobes rounded, porrect or recurved, glabrate, mostly with dense minute peltate trichomes, appearing whitish in bud; stamens four, staminode wanting, equal, inserted about 20 mm from the base of the tube, the filaments 50-55 mm long, anthers dorsifixed, inserted on the filament about halfway up, the thecae parallel, 7-10 mm long, slightly glandular pubescent; style ca. 8 cm long, the stigma situated at the corolla mouth, surrounded by the united anthers, ovary narrowly ovoid, sessile, minutely glandular papillose, 8-10 mm long, the disc annular-pulvinate, glabrous. Fruit ovoid or ellipsoid, 20-45 × 15-25 mm, with 4 dark grooves, dehiscing into two papery valves; the base enclosed in the calyx; fruiting calyx persistent, slightly spreading; seeds suborbicular, the body narrow, surrounded by a wing. Figures: Figure 2; Humboldt & Bonpland (1805-1817, vol. 1, fig. 65); Gentry (1977: 71 (as E. longiflorus)).

The characters used by Macbride (1961) and Sandwith (1965) to separate elements of this species into distinct taxa, corolla length and pubescence, are not diagnostic. There is great variation in dimensions and general appearance of flowers of this species, but the variation in most characters appears to be continuous, leading to the conclusion that a series of widely separated populations represent conspicuous variants of a single polymorphic species. Perhaps most conspicuous is corolla size and width in relation to calyx length. In some specimens (Prieto P-151, Davies 220), the corolla (10 cm long) greatly exceeds the calyx and is narrowly tubular throughout. Such a flower was illustrated as the type of Eccremocarpus longiflorus. In other cases, such as the flower illustrated as the type of E. viridis, the corolla is relatively broader, hardly or not exserted from the calyx. On one collection

(Davis 220), two flowers have long (9-11 cm) corollas and two have short (6 cm), barely exserted ones. Exsertion of the stamens is also variable; some collections (McPherson 13159) have the stamens included in the corolla mouth and in others (Vargas 5956) they are clearly exserted. Stamens are subequal in length. In Vargas 5956, the type of E. vargasianus, the longer pair of stamens is only about 1 mm higher than the shorter ones. In this specimen, the corolla is narrowest below the middle. In other collections, the corolla is narrowest above, near, or below the middle, and in some collections, it is evenly cylindrical, either straight or curved, for its entire length.

A difficulty in interpreting the significance of flower features in herbarium collections is the likelihood that collections were made at different stages of flower opening, as noted under E. huainaccapac above and by Sandwith (1965: 147). The material underlying E. lobbianus and the original illustration of E. viridis may represent young flowers and not the dimensions and shapes of flowers when they are fully unfolded. The type material of Eccremocarpus viridis at Madrid and Chicago lacks flowers (Sandwith, 1965) and an indication as to where it was collected. The species concept of Sandwith was therefore shaped largely by the two other collections he cited, which are thought to come from Muña in the Huanaco Department of Peru. Thus, if Eccremocarpus viridis were to be divided into two or more species, it is not clear what the separated elements should be called.

Distribution. This species is found in Colombia, Ecuador, and Peru mainly between 2700 and 3600 m elevation. Most Colombian collections are from the Cordillera Central. Collections from the northern part of the range, Colombia and Ecuador and northern Peru, are much more uniform in character than those from parts of Peru from where most synonyms were described.

This species appears to flower and fruit throughout the year.

Representative specimens (Eccremocarpus viridis). CO-LOMBIA. Caldas: Nevado Del Ruiz, Carr. Termales-Refugio, 3825 m, 19 Mar. 1972, Cleef & Hart 2500 (MO^{C)}, U^C); Tolima Las Mesetas, E slope of Mt. Tolima, 3600 m, 13 May 1932, Cuatrecasas 2743 (COL^C, K^{SC}). ECUADOR. Napo: 3200 m, 1977, de Vries s.n. (AAU^C). PERU. Cuzco: Urubamba, Penas a Kosniriti, 3600 m, 23 Mar. 1946, Vargas 5956 (K^{SC}, MO^{C)}).

Eccremocarpus sect. Calampelis (D. Don) A. DC., Prodr. 9: 238. 1845. Calampelis D. Don, Edinb. Phil. Jour. 7: 89. 1829. TYPE: Calampelis scaber (Ruiz & Pavón) Sweet = Eccremocarpus scaber Ruiz & Pavón.

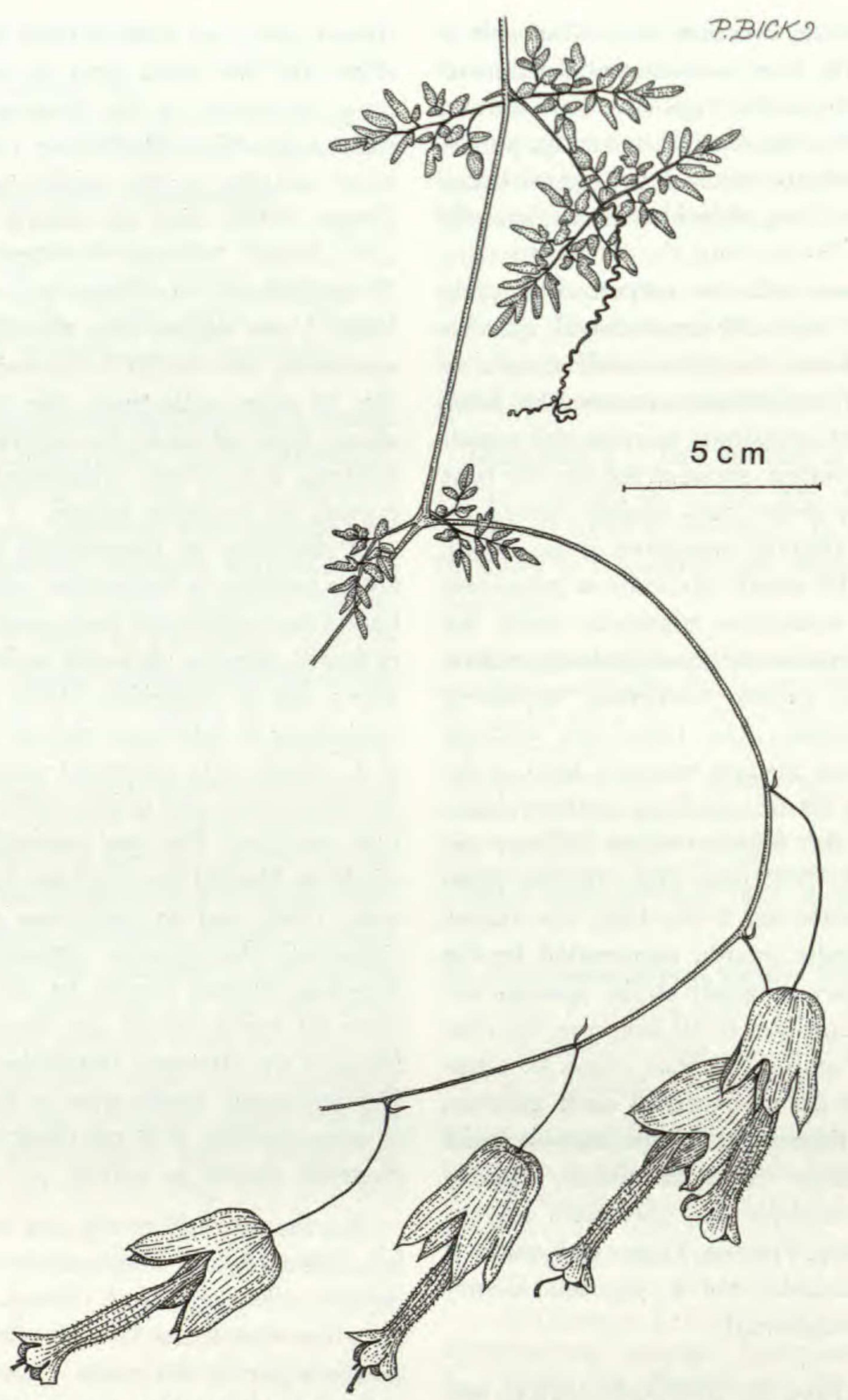


Figure 2. Eccremocarpus viridis Ruiz & Pavón. Inflorescence and leaves. After Vargas 5956 (type collection of E. vargasianus Sandw.).

3. Eccremocarpus scaber Ruiz & Pavón, Syst. Veg. 157. 1798. Calampelis scaber (Ruiz & Pavón) Sweet, Brit. Fl. Gard. ser. 2. 1. t. 30. 1831. [As "scabra."] TYPE: Chile. Provs. Colchagua, Rancagua, and San Jacob, Ruiz & Pavón 1798, (holotype, MA, photo, 029233, F).

Eccremocarpus sepium Bert. in "Merc. Chil. 1829" cf. Bull. Ferussac, 20. 111. 1830. Eccremocarpus scaber var. [b] saepium (Bert.) A. DC., Prod., 9: 239. 1845. TYPE: Chile. Sepibus secus, vias prope Rancagua S. Yago et Quillota, Bertero 965 (BM^G, F!, FI^S, MICH^G, MO^I, P^G). [Accepted as a synonym by Muñoz (1966).]

Eccremocarpus scaber var. aurea [sic] Benary, Gartenflora

22: 608. 1903. TYPE: cult. Hort. Schönbrunn (?W, not seen).

Eccremocarpus scaber var. carmineus [sic] Spigolatore, Bull. R. Soc. Toscana Orticultura 29(2): 339, fig. 22. 1904. TYPE: cultivated in ?France, not located.

Eccremocarpus scaber carmineus Pynaert, Rev. Hort. Belge 31: 55. 1905. TYPE: cult. Belgium, not located.

Eccremocarpus scaber var. roseus Huxley et al., New Roy Hort. Soc. Dict. Gard. 2: 122. 1992. TYPE: Not located.

Vine, climbing and twining, 2-6 m long, basally woody, the stem drying with alternating ridges and canals, puberulent with short, erect, often gland-tipped hairs and occasional weak hairs to 2 mm

long. Leaves opposite (sometimes one reduced or suppressed), generally 2-6 cm long, bipinnate with opposite pinnae, each with a terminal, mostly ternately-branched wiry tendril, usually with four primary mostly opposite pinnae, these with 3-5 leaflets, leaflets ovate to rhomboid, often oblique, 8-30 × 7-15 mm, basally cordate or truncate, apically obtuse, margins entire or dentate, shiny-grayish to dark green above, glabrate to pilose with short glandular hairs, mostly appearing as palmately 2-5-nervate; petiolules 2-5 mm long, often pubescent; petiole 2-6 cm long. Inflorescences opposite the leaves, sometimes appearing terminal, racemose, several to many flowered, to 25 cm long, pubescent with simple, mostly gland-tipped hairs; bracteoles 4-10 mm long, deltoid to linear and apically attenuate; pedicels 5-30 mm long. Flowers with the calyx red or orange (green), campanulate, ca. 8 × 4-8 mm, 5-dentate, unequally split 1/3-1/2 way down, puberulent with gland-tipped hairs; sometimes conspicuously nerved, corolla red or orange, sometimes yellowish near the tip, the tube subcylindrical, $20-25 \times 2-3$ mm wide at the base, expanded about 1/3 way up on one side to 5 mm across, contracted at the mouth, the lobes rounded, mostly recurved, glabrate, ca. 4 mm wide at the mouth; stamens four, unequal or (Muñoz) equal, 8 mm long, the filaments inserted about halfway up the corolla, then free or (Muñoz) united to about the middle of the thecae; anthers 2.4 mm long, the anther thecae basally divaricate or (Muñoz) parallel and united, the lobes of the stigma slightly expanded when closed (dried), slightly shorter than and surrounded by the anthers; ovary sessile, ovoid to conical, smooth except for two longitudinal ridges; disc annular-pulvinate, ca. 1 × 2.5 mm across, red (Muñoz). Fruit short-stipitate, ellipsoidal, 30-40 × 15-20 mm, glandular, with 4 dark grooves, dehiscing into two papery valves; fruiting calyx persistent and slightly curved away from the fruit base; fruiting peduncles 20-30 mm long; seeds 3-3.5 mm across, suborbicular, the body dark brown, ovoid, surrounded by a shiny, hyaline wing. Figures: Edward's Bot. Reg. (1825: t. 939*); Sweet, Brit. Fl. Gard. (1831: t. 30); Maund (1831*: 289*); Louden (1844: 1263*); Schumann (1894: fig. 93a, b); Benary (1903: 609); Spigolatore (1904: 340); Pynaert & Pynaert (1905: 55); Muñoz (1966*); Hay & Synge (1969: 247*); Hoffman J. (1978: 132*); Graf (1986: 184*); Tsukamoto (1988 vol. 3: 339*); Graf (1992: 270*); Huxley (1992: 1: 352); Belmonte et al. (1994). (* colored illustration.)

Two other names, Tourretia scabra Dombey and Dombeya nodiflora L'Her., were noted in the syn-

onymy of this species by De Candolle (1845), but they were not validly published.

Distribution. Low cordillera in Chile from Aconcagua to Valdivia, mainly between 1000 and 1800 m, but ranging from 300 to 3000 m elevation. The species is also found in Chubut and Rio Negro, Argentina. Gentry's database recorded two collections, Chavez 3467 and Shepard 9, from Cuzco and Puno Departments in Peru. The Chavez collection was labeled as a cultivated plant, and because Puno is so distant from the range of the species in central and southern Chile, the Shepard collection is also assumed to have been cultivated. Eccremocarpus scaber is occasionally cultivated outdoors in Europe as a curious ornamental. The species has been collected in flower in South America mainly from October to March, but plants in southern European gardens are said to bloom continuously (Spigolatore, 1904).

Plants of this species in European cultivation have displayed considerable variation of flower color, e.g., calyx green, corolla rose, dark red, scarlet to deep orange-red, orange, or golden (Loudon, 1844; Benary, 1903; Pynaert & Pynaert, 1905), although this variation has not been noted by Chilean writers (Muñoz, Hoffman, Navas). In addition to the names noted in synonymy under this species, Huxley (1992: 122) noted *Eccremocarpus* Anglia Hybrids, with flowers yellow, orange, pink, scarlet, and crimson, which are here considered to be forms of *E. scaber*.

Pollination of Eccremocarpus scaber is by hummingbirds as evidenced by notes on collections (Elliott 247) and the common name Chupa-chupa (Behn s.n., Elliott 247, Kausel 1673), a Spanish word for suck, as hummingbirds seem to do when their bills enter the flowers. A study of nectar and nectaries in Eccremocarpus scaber by Belmonte et al. (1994) noted pollination by Giant Humming-birds (Patagonia gigas gigas).

The climbing ability of this species by means of tendrils with tactile responses has long been subject of study (Darwin, 1891; Junker & Reinhold, 1975; Tronchet, 1977; Junker, 1977).

Representative specimens (Eccremocarpus scaber). ARGENTINA. Chubut: entre El Bolsón y Lago Puelo, 42°05′S, 71°38′W?, 13 Nov., Meyer 9422 (K^{SI}). CHILE. Colchagua: Cuming 21 (BM^G). Curico: Curico, Los Quenes (Andes de Curico), 35°01′S, 70°48′W, 1000 m, 20 Jan. 1942, Aravena 33365 (MO^{GI}). Santiago: Tiltil, 33°55′S, 70°57′W, 840 m, 9 Nov. 1941, Behn 21492 (K^{SI}). Valdivia: Buchtien s.n. (L^G). Valparaiso: Quebrada Cale, 33°S, 71°W, 1 Mar. 1952, Boelcke 6474 (F^I, MO^{GI}, MO^{GI}). PERU. Puno: Lake Titicaca, 15°48′S, 69°24′W, 3125 m, 26 Nov. 1919, Shepard 9 (NY^{GI}).

REJECTED NAMES

Eccremocarpus ruber Regel, Cat. Pl. Hort. Aksakov. 51. 1860. Nomen nudum.

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LIST OF COLLECTIONS

Specimens are listed alphabetically by principal collector and number, followed by herbarium acronym. Identifications are indicated by numbers: 1, Eccremocarpus huainaccapac; 2, E. viridis; 3, E. scaber. Differing identifications made by previous workers follow in parentheses: the species epithet and the workers' initials: G: A. H. Gentry, S: N. S. Sandwith.

Without collector, number (F!) 3. Without collector, number (MO!) 3 EUROPE. Without collector, number (NY!) 3.

Anderson s.n. (MO¹) 3 EUROPE, England. Aravena 33316 (MOc¹) 3 CHILE. Curico. Aravena 33365 (MOc¹) 3 CHILE. Curico. Ball s.n. (NYc¹) 3 CHILE. Santiago. Behn s.n. (F¹) 3 CHILE. Behn 21492 (K¹) 3 CHILE. Santiago. Bertero s.n. (NYc¹, PG) 3 CHILE. Bertero 231 (PG) 3 CHILE. Bertero 239 (FIS) 3 CHILE. Valparaiso. Bertero 965 (BMG, MICHG, MO¹, PG) 3 CHILE. Valparaiso. Bocher et al. 598 (CG) 3 CHILE. Santiago. Boelcke 6474 (F¹, MOG¹) 3 CHILE. Valparaiso. Bridges 177 (K¹, PG) 3 CHILE. Buchtien s.n. (LG) 3 CHILE. Valdivia.

Calvert s.n. (BM^{GI}) 3 CHILE. Valparaiso. Canby s.n. (NY^{GI}) 3 CHILE. Chavez 3467 (MO^{GI}) 3 PERU. Cuzco. Cleef & Hart 2500 (MO^{GI}, U^G) 2 (longiflorus-G) COLOM-BIA. Caldas. Comber 1011 (K^I) 3 CHILE. Cook & Gilbert 1237 (US?) 2 (longiflorus-MacBride) PERU. Cuzco. Contreras? & Veitch 218 (K^{GG}) 2 PERU. Crovetto 3276 (F^I) 3 ARGENTINA. Chubut. Cuatrecasas 2743 (COL^G, K^{GG}) 2 (mutisianus-G,S) COLOMBIA. Tolima. Cuatrecasas 9330 (COL^G, F-3^I) 2 (longiflorus-G) COLOMBIA. Caldas. Cuatrecasas 9351B (COL^G) 2 (longiflorus-G) COLOMBIA. Caldas. Cuatrecasas 20400 (F-3^I) 2 COLOMBIA. Valle. Cuming 21 (BM^G) 3 CHILE. Colchagua. Cuming 615 (K^I) 3 CHILE. Valparaiso.

Davis (Davies) s.n. (MO^{G!}, BM^{SG}) 2 PERU. Huánuco. Davis comm. Veitch 220 (K^{S!}) 2 PERU. Huánuco. Dave 860 (K^S, NY^{G!}) 2 (longiflorus-G,S) COLOMBIA. De Barba 487 (F[!]) 3 ARGENTINA. Chubut. Devia & Prado 1880

(MO^{G!} ex TULV) 2 (longiflorus-G) COLOMBIA. Valle. de Vries s.n. (AAU^G) 2 (longiflorus-G) ECUADOR. Napo. Dombey s.n. (P^G) 3 CHILE. Santiago.

Ellenberg 4867 (MO^{c!}) 2 (vargasianus-¹) PERU. Elliott 419 (BM^c) 3 CHILE. Elliott 247 (K¹) 3 CHILE. Elwes s.n.

(K') 3 CHILE.

Fournier s.n. (Psc) 2 (longiflorus-G,S) ECUADOR. Pichincha. Frbr. Bert. Jime. ? s.n. (MO^{G!}) 3 CHILE. Freire et al. 656 (QCA^G) 2 (longiflorus-G) ECUADOR. Chimborazo. Frödin s.n. (NY^{G!}) 3 CHILE. Santiago. Frödin 635 (BM^G) 3 CHILE. Aconcagua.

Gay s.n. (K^s) 2 (longiflorus-S) ECUADOR. Gay s.n. (P^c) 3 CHILE. Santiago. Gay s.n. (P^c) 3 CHILE. Valdivia. Gay 20 (P^c) 3 CHILE. Santiago. Goodspeed 16853 (MO^t) 3 CHILE. Aconcagua. Goodspeed 23344 (K^t) 3 CHILE.

Aconcagua.

Halpin s.n. (CLEMS^c, K^c) 3 CHILE. Hartweg 148 (K^t) 2 (longiflorus-G,S) ECUADOR. Loja. Harvey s.n. (Kst) 3 CHILE. Hastings 171 (NY^{ct}) 3 CHILE. Hirsch P1022 (K^t) 2 (vargasianus-S) PERU. Urubamba. Hort. Vilmourin s.n. year 1857 (MO^t) 3 EUROPE. France. Humboldt s.n. (K^s, MO^t, P^{sc}) 2 (longiflorus-G,S) PERU. Loja.

Jameson s.n. (K^{SG}) 2 (longiflorus-S) ECUADOR. Pichincha. Jameson 56 (NY^{G!}) 2 (longiflorus-G) ECUADOR. Pichincha. Jameson 186 (K^{SG!}) 2 (longiflorus-S) ECUADOR. Pichincha. Jameson 286 (BM^{SG}, F^G, K, NY^G,

Psc) 2 (longiflorus-G,S) ECUADOR. Pichincha.

Karsten s.n. (W^S) 2 (longiflorus-S) COLOMBIA. Pichincha. Karsten s.n. (W^S) 2 (longiflorus-S) ECUADOR. Cundinamarca. Kausel 1673 (F^I) 3 CHILE. Santiago. King 589 (BM^G) 3 CHILE. King 712 (BM^G) 3 CHILE. Kuntze s.n. (NY^{GI}) 3 CHILE.

Leeds s.n. (F') 3 U.S.A. California. Lehmann 3149 (BMsc, Ks!) 2 (longiflorus-G,S) COLOMBIA. Caldas. Lobb 391 (Ks!) 2 (lobbianus-S) PERU. Londono et al. 481 (MOs! ex-MEDEL) 2 (longiflorus-G) COLOMBIA. Antioquia. Luteyn & Tirira 1336A (MO!) 2 ECUADOR. Napo.

Macbride 4371 (F¹, Ws) 2 PERU. MacLean s.n. (K-3s¹) 2 (lobbianus-S) PERU. Macrare? s.n. (K¹) 3 CHILE. Mathews 3176 (BMsc, K¹) 2 (longiflorus-G,S) PERU. Amazonas. Mathews s.n. (BMsc) 2 (longiflorus-S) PERU. Amazonas. Mazzei s.n. (FIc) 3 CHILE. Santiago. Mc-Pherson 13159 (MOc¹) 2 (longiflorus-G) COLOMBIA. Antioquia. Menzies 91 (MOc¹) 3 CHILE. Mexia 7887 (BMc, F¹, MOc¹, NYc¹) 3 CHILE. Curico. Meyen s.n. (Pc) 3 CHILE. Meyer 9422 (Ks¹) 3 ARGENTINA. Chubut. Middleton s.n. (BMc) 3 CHILE. Molau & Ohman 1635 (GBc) = photocopy MOc¹) 2 (vargasianus-G) PERU. Cuzco. Montero 67a (MOc¹) 3 CHILE. Colchagua. Montero 260 (K¹) 3 CHILE. Santiago. Montero 507 (MOc¹) 3 CHILE. Santiago. Morrison 16853 (MOc¹) 3 CHILE. Aconcagua.

Nuñez & Galiano 13414 (MO!) 1 PERU. Cuzco. Nuñez & Luna 8841 (F!, MOG!) 2 (vargasianus-G!) PERU. Cuzco. Nuñez et al. 14135 (MOG!) 1 PERU. Apurimac.

Øllgaard et al. 38199 (AAU^c) 2 (longiflorus-G) EC-UADOR. Chimborazo. Øllgaard et al. 98155 (AAU^c) 2 (longiflorus-G) ECUADOR. Carchi. Ortiz s.n. (AAU^c, QCA^c) 2 (longiflorus-G) ECUADOR. Imbabura. Ortiz 30 (AAU^c, NY!) 2 (longiflorus-G) ECUADOR.

Pearce 533 (K^{SI}) 2 PERU. Huánuco. Pearce 823 (K^{SI}) 2 (vargasianus-S) PERU. Penland & Summers 1080 (F^I) 2 ECUADOR. Azuay. Pennell 12262 (F^I, GH, NY^{GI}) 3 CHILE. O'Higgins. Philippi s.n. (HB^G) 3 CHILE. Santiago. Poeppig 2 (BM^G) 3 CHILE. Prance 26595 (US^G) 2 (longiflorus-G) ECUADOR. Napo. Prieto P-151 (NY^{GI}= MO, photocopy) 2 (longiflorus-G, Wurdack) ECUADOR. Cañar. Purdie s.n. (PSG, K-2SI) 2 (longiflorus-G,S) CO-LOMBIA. Risaralda.

Rauh & Hirsch P.1022 (K^s) 2 (vargasianus-S) PERU. Urubamba. Raddin s.n. (F^t) 3 CHILE. Santiago. Reed s.n. (K^t) 3 CHILE. Maule. Rossiter 398253 (MO^t) 3 NEW ZEALAND. Ruiz & Pavón 5/14 (MA-3^s, BM) 2 PERU. Ruiz & Pavón s.n. (BM^s, F^t ex MA, FI^s) 3 CHILE. Santiago.

Sanderness 288 (K!) 3 CHILE. Saunders 776 (KS!) 1 PERU. Apurimac. Schlatzer s.n. (AAU^G) 3 CHILE. Santiago. Schmidt s.n. (HB^G) 3 CHILE. Shepard 9 (NY^{G!}) 3 PERU. Puno. Simpson s.n. (P^G) 3 CHILE. Sodiro s.n. (P^{SG}) 2 (longiflorus-G,S) COLOMBIA. Cundinamarca.

Triana s.n. (Psc, COLc) 2 (longiflorus-G,S) COLOMBIA.

Antioquia. Triana 223 (Psc) 2 (longiflorus-G,S) COLOMBIA.

BIA. Risaralda. Triana 4107 (?5107,?8107,?4107)

(COLc, Psc) 2 (longiflorus-G,S) COLOMBIA. Cundinamarca.

Vargas 3034 (K^S, US^{SG}) 1 PERU. Cuzco. Vargas 5956 (K^{SI}, MO^{GI}) 2 (vargasianus-G,S) PERU. Cuzco. Vargas 20079 (MO^{GI}) 2 (vargasianus-G) PERU. Cuzco. Vargas 22644 (MO^{GI}) 2 (vargasianus-G) PERU. Cuzco. Vieillard 84 (P^G) 3 CHILE. Valparaiso.

Weberbauer (F?) 2 (longiflorus-Macbride, S) PERU. Cajamarca. Weberbauer 4938 (?) 2 (longiflorus-Macbride, S) ECUADOR. Werdermann 482 (BM^c, F!, HB^c, MO^{c!}, U^c) 3 CHILE. Santiago. Wildenow s.n. (HB^c) 3 CHILE.

Zöllner 6486 (L^c) 3 CHILE. Aconcagua. Zöllner 9350 (MO^{ci}) 3 CHILE. Valparaiso. Zöllner 11052 (MO^{ci}) 3 CHILE. Santiago.

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